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Homology and terminology of higher teleost postcleithral elements

Michael D. Gottfried

Museum of Natural History and Department of Systematics and Ecology, Dyche Hall, University of Kansas, Lawrence, Kansas 66045-2454; Field Associate, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112, USA

Abstract. Primitively, actinopterygians have a single postcleithrum, which is not homologous to the anocleithrum of sarcopterygians. The possession of multiple postcleithra is a shared derived feature of teleosts. Three to five postcleithra are typically found in lower teleosts; as many as seven are present in primitive fossil forms. Consideration of the positional relationships of postcleithra in primitive teleosts provides criteria for homologizing and naming teleost postcleithra. Ctenosquamate teleosts (myctophiforms and acanthomorphs) typically possess two postcleithra; on the basis of positional relationships these are interpreted as postcleithra two and three (not "one and two," "upper and lower," "dorsal and ventral," or "proximal and distal" as in previous interpretations). Ctenosquamates are therefore derived in having lost postcleithrum one, which is considered here to be the homologue of the single postcleithrum of primitive actinopterygians.

Introduction

The postcleithral elements of actinopterygian fishes are small dermal bones that lie along the posterior border of the pectoral girdle. Primitively, actinopterygians have a single, relatively small postcleithrum located at and extending dorsal to the juncture between the supracleithrum and cleithrum and lying medial to those two bones. This single postcleithrum can be seen in the Devonian genus *Cheirolepis* (Pearson and Westoll 1979), which is the most primitive actinopterygian according to recent analyses (Lauder and Liem 1983, Gardiner 1984). It is also present in the following lower actinopterygian groups: Cladistia (*Polypterus*, Jollie 1984b), Chondrostei (*Polyodon*, Gregory 1933), Ginglymodi (*Lepisosteus*, Jollie 1984a), and Halecomorphi (*Amia*, Figure 1A); the last is the sister taxon of the Teleostei (Schultze and Wiley 1984).

Extant lower teleosts typically have three postcleithra (Gosline 1980), with the most dorsal occupying the same relative position as the single postcleithrum of lower actinopterygians and the additional postcleithra a more ventral position. As many as six (possibly seven) postcleithra have been described by Arratia (1984, 1987) in the unusual Jurassic teleost *Varasichthys*, while five are known in several other Jurassic forms including *Bobbichthys*, *Protoclupea*, and *Domeykos* (Arratia 1987) and in juvenile *Salmo* (Arratia and Schultze 1987). Five postcleithra are also found in extant *Elops* (Figure 1B); Gosline (1980) referred to the two most ventral postcleithral elements in *Elops* as axillary scales, but Arratia (1984) considered them to be true postcleithra on the basis of their structure and lack of scale-like ornamentation.

While the exact number of postcleithra primitive for teleosts is not certain (because of poor phylogenetic resolution at the base of the Teleostei), and reduction in number or complete loss of postcleithra has occurred within different teleost groups (Gosline 1980), it is most parsimonious to hypothesize multiple postcleithra (probably five) as a teleost synapomorphy.

The ctenosquamate teleosts (myctophiforms and acanthomorphs; Rosen 1973) characteristically possess two postcleithra. The intent of this paper is to provide positional and phylogenetic criteria for homologizing teleost postcleithra and to determine which elements are represented in ctenosquamates.

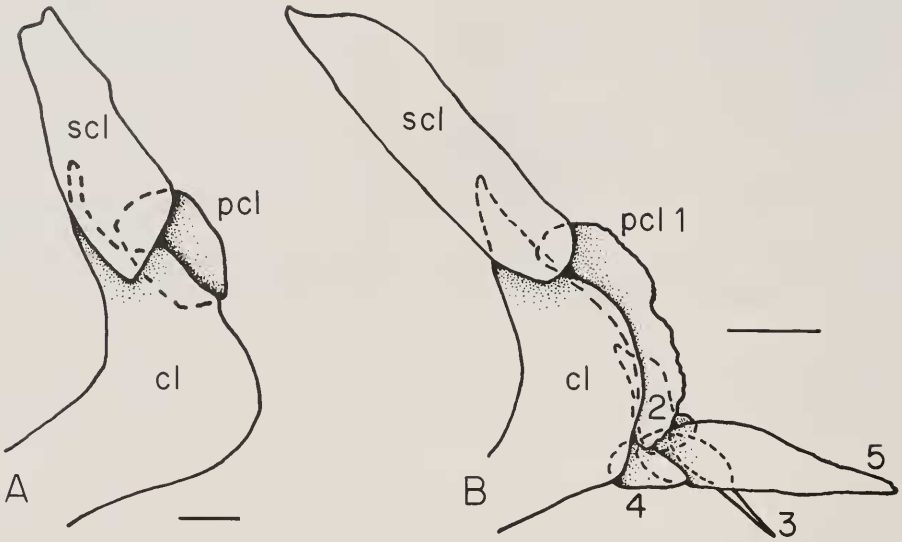

FIGURE 1. A, lateral view of the pectoral girdle in a lower actinopterygian, *Amia calva*, KU 1798 (note single postcleithrum positioned at supracleithrum/cleithrum juncture). B, lateral view of the pectoral girdle of a primitive teleost, *Elops saurus* (note multiple postcleithra); after Arratia and Schultze (1987). Scale bars = 5 mm. Abbreviations: cl, cleithrum; pcl, postcleithrum; scl, supracleithrum. Numbers 2–5 in B indicate postcleithra 2–5.

POSTCLEITHRAL TERMINOLOGY

The multiple postcleithra of teleosts have been subjected to a variety of different terminologies based on their relative positions, have been referred to as a "postcleithrum plus postpectorals" (Jollie 1986), or have been numbered. The numbering approach is preferable for three reasons: it allows for reference to multiple postcleithra without resort to awkward names (e. g., the "upper middle postcleithrum" or "middle ventral postcleithrum"), it permits a less ambiguous terminology that facilitates comparisons between the postcleithra of different forms, and it avoids using another name (the "postpectorals" of Jollie) for elements that in the past have consistently been called postcleithra.

The following positional relationships and suggested terminology are based on the location of the postcleithral elements in primitive teleosts such as the Jurassic forms discussed by Arratia (1987) and extant *Elops* (Figure 1B). The most dorsal postcleithrum in teleosts, which is interpreted here as homologous to the single postcleithrum of lower actinopterygians, is most appropriately referred to as postcleithrum 1. It lies at the level of and extends dorsal to the juncture between the supracleithrum and cleithrum and, depending on the taxon, extends ventrally to a variable degree. It is usually overlapped by a portion of the cleithrum and the most ventral part of the supracleithrum. Postcleithrum 2 articulates dorsally with the ventromedial margin of postcleithrum 1 and lies at approximately the level of the middle region of the cleithrum, medial to the scapula and coracoid. It does not extend as far dorsally as the juncture between the cleithrum and supracleithrum. In some forms a gap separates postcleithra 1 and 2 (Gosline 1980). Postcleithrum 3 characteristically forms a slender spinous process that angles posteroventrally, medial to the pectoral fin. Its somewhat stouter dorsal portion articulates with the anteromedial surface of postcleithrum 2. Postcleithrum 3 is a useful landmark element and can generally be distinguished by its spinelike appearance and posteroventrally angled orientation; in contrast, the other postcleithral elements are more flattened and scalelike and often have a crenulated surface .

Postcleithra 4 through 6 (or 7) form an additional series of sequentially overlapping elements that extend back from the lower posterior corner of the cleithrum, lateral to postcleithra 2 and 3. Postcleithra 4 and 5 are found in *Elops* (Figure 1B), in juvenile *Salmo*

(Arratia and Schultze 1987), and in several Jurassic forms discussed by Arratia (1987); as many as six (possibly seven) are known only in the Jurassic genus *Varasichthys*.

Results and Discussion

As noted above, ctenosquamate teleosts generally possess two postcleithral elements. Exceptions to this exist; e. g., among acanthomorph ctenosquamates some gobioids may lack either of the two elements or lack postcleithra entirely (Springer 1983), and some acanthurids have only a single postcleithrum (Johnson and Washington 1987). Previous literature shows that there has been confusion and a lack of consistency as to which postcleithra these are and what they should be called. Some authors (Patterson 1964, Zehren 1979, both referring to beryciforms; Springer 1983, referring to gobioids) call these two bones the "dorsal and ventral" postcleithra, while others refer to them as "upper and lower" postcleithra (Rosen and Patterson 1969, referring to "paracanthopterygians"), "postcleithra 1 and 2" (e. g., Greenwood 1976, 1985, Braga and Azpelicueta 1982, Arratia 1982, Kong 1985, all referring to various acanthopterygians), or "proximal and distal" postcleithra (Kullander 1988, referring to cichlids).

Examination of the pectoral girdle in a variety of acanthomorph ctenosquamates (see "Materials Examined" and Figure 2) confirms that two postcleithra are typical in the group, as noted by Gosline (1980). In addition, non-acanthomorph ctenosquamates typically have two postcleithra; these include *Polymixia* (Zehren 1979), the sister taxon of the Acanthomorpha according to Rosen (1985) and Stiassny (1986), and myctophiforms (Goody 1969, Paxton 1972), the sister group of *Polymixia* plus the Acanthomorpha (Rosen 1985, Stiassny 1986).

The two postcleithra in the various ctenosquamates generally occupy the same relative positions and have comparable proportions. The more dorsal of the elements is flattened and platelike, lies at approximately the level of the middle region of the cleithrum (and medial to the scapula and coracoid), is overlapped (to varying degrees) by the cleithrum, and does not lie as far dorsally as the most dorsal postcleithrum in primitive teleosts. The more ventral element is generally narrower, posteroventrally directed, medial to the pectoral fin, and terminates in a pointed process. It articulates dorsally with the anteromedial surface of the postcleithrum above it. In some forms, for example, *Prionotus* (Triglidae, Percomorpha) and *Cottus* (Cottidae, Percomorpha; Figure 2C), the more dorsal postcleithrum is also relatively narrow and spinelike.

The positional relationships described earlier indicate that the two postcleithral elements in ctenosquamates are best interpreted as postcleithra 2 and 3. This means that the other terminologies are unneccessarily imprecise. More important, it follows from this interpretation that postcleithrum 1 (the teleost homologue of the single postcleithrum of lower actinopterygians) has been lost in ctenosquamates, and the "postcleithra 1 and 2" terminology is therefore inappropriate for the group.

Although the determination of the elements in ctenosquamates as postcleithra 2 and 3 is relatively straightforward, it is neccessary to add one cautionary note. I observed ontogenetic fusion in the postcleithra of a cleared and stained series (n = 17) of *Cichlasoma citrinellum* (Percomorpha, Cichlidae); specimens ranged from small juveniles to large adults (35 mm to 145 mm total length). Juveniles and sub-adults of *C. citrinellum* have two distinctly separate postcleithral elements up to approximately 70–90 mm in total length (Figure 3A). The more dorsal of these (postcleithrum 2) is flattened and has a semilunate shape. A thickened spinelike ridge runs along the anterior edge of the element, terminating dorsally in a sharp point. Posterior to the ridge the bone is thin and has a crenulated surface similar to that of elements in the opercular series. The ventrally positioned element (postcleithrum 3) is more robust and tapers ventrally to a sharp point. The two bones articulate by means of a shallow depression on the dorsolateral surface of postcleithrum 3 into which fits the rounded lower corner of postcleithrum 2.

In contrast, adults of *C. citrinellum* have what appears to be a single postcleithrum (Figure 3B). In these larger fish, the anteriorly positioned ridge of postcleithrum 2 has grown down onto postcleithrum 3, and there is no longer any indication of an articulation or that the

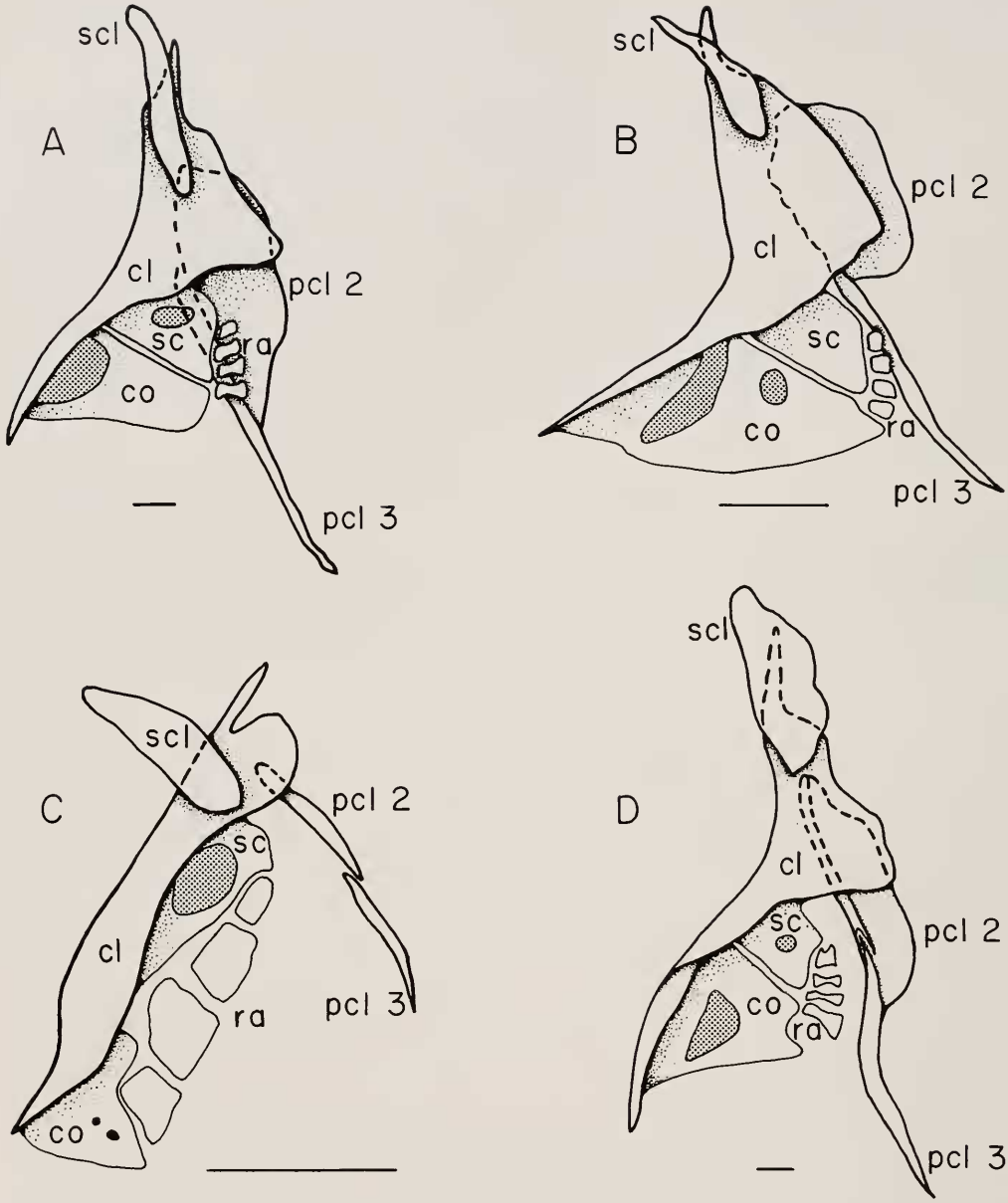

FIGURE 2. Lateral views of the pectoral girdles of ctenosquamate teleosts. A, *Percopsis omiscomaycus*, KU 11337 ("Paracanthopterygii," Percopsiformes, Percopsidae). B, *Goodea atripinnis*, KU 16998 (Acanthopterygii, Atherinomorpha, Atherinidae). C, *Cottus bairdi*, KU 17151; note reduced pcl 2 (Acanthopterygii, Percomorpha, Cottidae). D, *Lepomis gibbosus*, KU 13983 (Acanthopterygii, Percomorpha, Centrarchidae). Scale bars = 2 mm. Abbreviations: cl, cleithrum; co, coracoid; pcl 2, 3, postcleithrum 2, 3; ra, pectoral fin radials; sc, scapula; scl, supracleithrum.

two elements were once separate. Similar ontogenetic fusion of postcleithra 2 and 3 has been observed in the acanthuroid percomorph *Zanclus cornutus* (Johnson and Washington 1987).

The most parsimonious interpretation of the loss of postcleithrum 1 in ctenosquamates is that it represents an additional synapomorphy corroborating monophyly of the group [see Lauder and Liem (1983) and Stiassny (1986) for additional ctenosquamate synapomorphies].

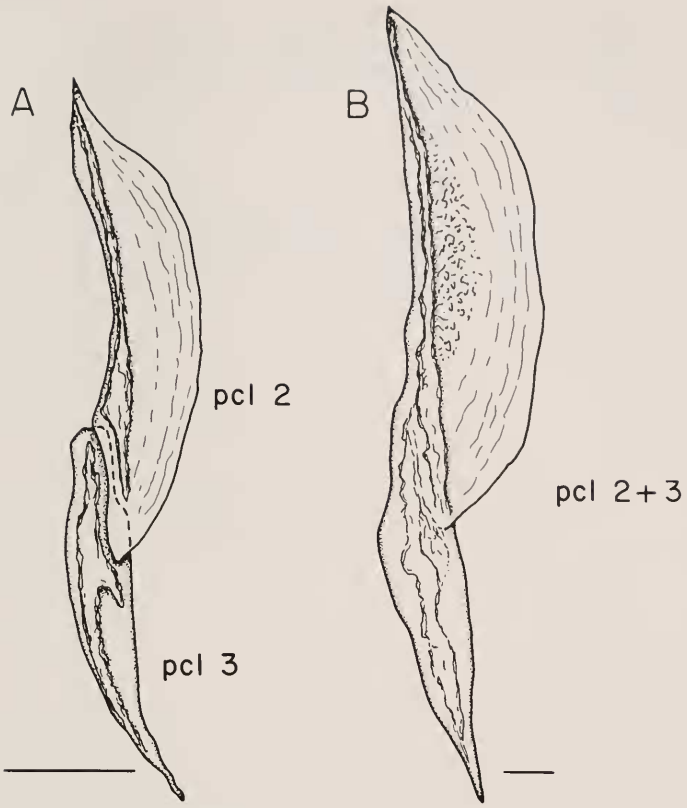

FIGURE 3. Left lateral views of postcleithra (pcl) of *Cichlasoma citrinellum* (Acanthopterygii, Percomorpha, Cichlidae). A, from a juvenile (37 mm total length) in which pcl 2 and 3 are separate (KU 21916). B, from an adult (118 mm total length) in which pcl 2 and 3 are fused (KU 21915). Scale bars = 1 mm.

The primitive condition relative to that in ctenosquamates is possession of postcleithra 1, 2, and 3. Postcleithra 1 through 3 are present in close ctenosquamate outgroups, including the order Aulopiformes (Sulak 1977, Gosline 1980), which is the sister group of the ctenosquamates according to Lauder and Liem (1983), Rosen (1985), and Hartel and Stiassny (1986). Sulak (1977) did describe two synodontid aulopiforms (*Synodus* and *Trachinocephalus*) as having two postcleithra, which occupy the positions of postcleithra 2 and 3 by my interpretation. However, Sulak (1977, p. 68) suggested that three postcleithra are typical for the group, and basal aulopiforms (e. g., *Aulopus*) have three postcleithra, so the loss of a postcleithrum in some aulopiforms can be interpreted as independent of the loss in ctenosquamates. Postcleithra 1 through 3 are also present in further outgroups, including salmoniforms, clupeomorphs (Gosline 1980), and characiforms (e. g., *Brycon*, Weitzman 1962).

Mapping postcleithral conditions on to an existing hypothesis of actinopterygian interrelationships (Figure 4) indicates that the interpretation here is consistent with the phylogenetic concept of homology as discussed by Ax (1987). Remane (1952) considered a positional relationship such as I have used to be the strongest criterion for establishing homology.

Gosline (1980) interpreted the most dorsal postcleithrum of lower teleosts and the single postcleithrum of lower actinopterygians as homologues of the anocleithrum of sarcopterygians (lungfishes, coelacanths, and crossopterygians). I agree with Gardiner (1984) that the single postcleithrum of lower actinopterygians should not be considered homologous to the anocleithrum, the possession of which has been interpreted as a sarcopterygian synapomorphy

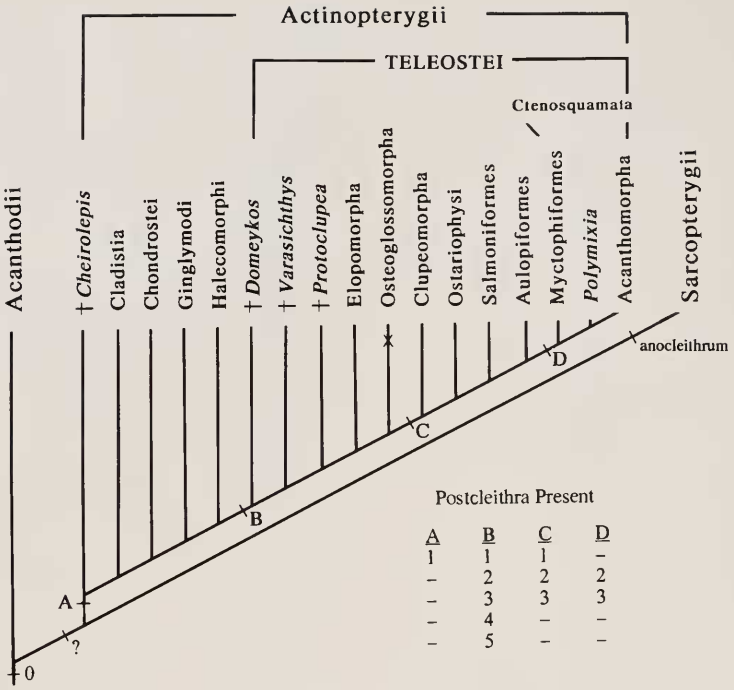

FIGURE 4. Phylogenetic diagram of the major groups of actinopterygians, with postcleithral conditions specified at the appropriate levels. A, single postcleithrum present at juncture of supracleithrum and cleithrum (the primitive actinopterygian condition); B, multiple postcleithra (1 through 5), hypothesized here as a teleost synapomorphy, with postcleithrum 1 the homologue of the single postcleithrum of lower actinopterygians and 2–5 in a more ventral position; C, reduction to postcleithra 1–3; D, reduction to postcleithra 2–3, with loss of postcleithrum 1 interpreted as a ctenosquamate synapomorphy; X, independent reduction to a single postcleithrum in the Osteoglossomorpha. ?, primitive condition unknown for the Osteichthyes (Actinopterygii plus Sarcopterygii); 0, postcleithra absent. Lower right, postcleithra present at the stem of each indicated node within the Actinopterygii. Note presence of anocleithrum (here considered nonhomologous to postcleithrum 1) in Sarcopterygii. †, taxa represented by fossils only. Sequence of taxa primarily based on Lauder and Liem (1983) and Arratia (in press) for the lower teleostean groups.

(Long 1989). In sarcopterygians, the anocleithrum lies fully within the arcade of pectoral girdle elements, articulating dorsally with the supracleithrum and ventrally with the cleithrum and preventing those two elements from contacting one another. In the most primitve actinopterygians, *Cheirolepis* (Pearson and Westoll 1979) and Cladistia (Jollie 1984b), the postcleithrum has a different position; it lies along the posterior edge of the pectoral girdle, where it is overlapped by the supracleithrum and cleithrum, which are in contact. The distinction between the anocleithrum and postcleithrum is further clarified by Jollie's (1984a) observations on the developmental osteology of the extant ginglymodian *Lepisosteus*, in which the postcleithrum (in juveniles) first forms as a dermal ossification separate from and posterior to the pectoral girdle and only later in development contacts and is overlapped by (but does not separate) the supracleithrum and cleithrum. The primitive condition for the Osteichthyes (Actinopterygii plus Sarcopterygii) is not known because of lack of information on the osteichthyan sister group, the Acanthodii (Figure 4).

Finally, teleost groups other than ctenosquamates reduce the number of postcleithra. Siluriforms, mormyrids, anguillids, and engraulids lack postcleithra entirely (Gosline 1980); most osteoglossomorphs (Taverne 1977, 1978) and some cyprinids (Gosline 1980) have a single postcleithrum. These reductions can best be interpreted as independent losses within each lineage.

Materials Examined

The following specimens were examined for this study. Except where noted, specimens are cleared and stained (for cartilage and bone); they are in the Ichthyology Division of the University of Kansas Museum of Natural History (KU). Numbers in parentheses indicate number of individuals per lot.

Actinopterygii, Halecomorphi;
Amia calva, KU 1798 (1; skull only)
Teleostei, Percopsiformes, Aphredoderidae;
Aphredoderus sayanus, KU 12590 (1; cleared only)
Percopsiformes, Percopsida
Percopsis omiscomaycus, KU 11337 (1; in alcohol)
Gadiformes, Gadidae;
Microgadus proximus, KU 12150 (1; in alcohol)
Atherinomorpha, Atherinidae;
Basilichthys australis, KU 19278 (7)
Goodea atripinnis, KU 16998 (5)
Labidesthes sicculus, KU 17621 (7)
Atherinomorpha, Cyprinodontidae;
Fundulus catenatus, KU 17616 (7)
Crenichthys baileyi, KU 11862 (11)
Percomorpha, Percidae;
Stizostedion canadense, KU 17920 (1)
Percomorpha, Percichthyidae;
Morone chrysops, KU 18024 (5)
Percomorpha, Sciaenidae;
Aplodinotus grunniens, KU 21461 (8)
Percomorpha, Cottidae;
Cottus bairdi, KU 17151 (7)
Percomorpha, Triglidae;
Prionotus evolans, KU 21435 (2)
Percomorpha, Centrarchidae;
Elassoma zonatum, KU 20307 (5)
Micropterus salmoides, KU 15939 (2)
Lepomis gibbosus, KU 13983 (4)
Percomorpha, Cichlidae;
Cichlasoma citrinellum, KU 21915 (1), 21916 (1), 21917 (15)

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Literature Cited

Arratia, G. 1982. A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Perciehthyidae, and Percilidae). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 540:1–52.

———. 1984. Some osteological features of *Varasichthys ariasi* Arratia (Pisces, Teleostei) from the Late Jurassic of Chile. Paläontologische Zeitschrift 58:149–163.

———. 1987. Jurassic fishes from Chile and critical comments. Pp. 257–286 *in* W. Volkheimer and E. A Musacchio (eds.). Biostratigrafía de los Sistemos Regionales del Jurásico y Cretácico en America del Sur, Tomo 1. Jurásico anterior a los movimientos málmicos. Mendoza, Argentina; Comité Sudamericano del Jurásico y Cretácico.

———. In press. The caudal skeleton of Jurassic teleosts: a phylogentic analysis. Special Symposium Volume. Early Vertebrates and Related Problems in Evolutionary Biology. Academia Sinica, Beijing.

Arratia, G., and H.-P. Schultze. 1987. A new halecostome fish (Actinopterygii, Osteichthyes) from the Late Jurassic of Chile and its relationships. Dakoterra 3:1–13.

Ax, P. 1987. The Phylogentic System. The Systematization of Organisms on the Basis of Their Phylogenesis. Wiley, New York.

Braga, L., and M. Azpelicueta. 1982. Estudio sobre *Plagioscion ternetzi* Boulenger, 1895. (Perciformes, Sciaenidae). Parte II. Neotropica 28:103–116.

Gardiner, B. G. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. Bulletin British Museum of Natural History (Geology) 37:173–428.

Goody, P. C. 1969. The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids. Bulletin British Museum of Natural History (Geology), Supplement 7:1–255.

Gosline, W. A. 1980. The evolution of some structural systems with reference to the interrelationships of modern lower teleostean fish groups. Japanese Journal of Ichthyology 27:1–28.

Greenwood, P. H. 1976. A review of the family Centropomidae (Pisces, Perciformes). Bulletin of the British Museum (Natural History, Zoology) 29:1–81.

———. 1985. Notes on the anatomy and phyletic relationships of *Hemichromis* Peters 1858. Bulletin of the British Museum (Natural History, Zoology) 48:131–171.

Gregory, W. K. 1933. Fish skulls. A study of the evolution of natural mechanisms. Transactions of the American Philosophical Society 23:75-481.

Hartel, K. E., and M. L. J. Stiassny. 1986. The identification of larval *Parasudis* (Teleostei, Chlorophthalmidae); with notes on the anatomy and relationships of aulopiform fishes. Breviora 487:1–23.

Johnson, G. D., and B. B. Washington. 1987. Larvae of the Moorish idol, *Zanclus cornutus*, including a comparison with other larval acanthuroids. Bulletin of Marine Science 40:494–511.

Jollie, M. 1984a. Development of cranial and pectoral girdle bones of *Lepisosteus* with a note on scales. Copeia (1984): 476–502.

———. 1984b. Development of the head and pectoral skeleton of *Polypterus* with a note on scales (Pisces, Actinopterygii). Journal of Zoology (London) 204:469–507.

———. 1986. A primer of bone names for the understanding of the actinopterygian head and pectoral girdle skeletons. Canadian Journal of Zoology 64:365–379.

Kong, I. 1985. Revision de las especies chilenas de *Sebastes* (Osteichthyes, Scorpaeniformes, Scorpaenidae). Estudios Oceanología 4:21–75.

Kullander, S. O. 1988. *Teleocichla*, a new genus of South American rheophilic cichlid fishes with six new species. Copeia (1988): 196–230.

Lauder, G. V., and K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes. Bulletin Museum of Comparative Zoology 150:95–197.

Long, J. A. 1989. A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. Journal of Vertebrate Paleontology 9:1–17.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. Philosophical Transactions of the Royal Society (B) 247:213–482.

Paxton, J. R. 1972. Osteology and relationships of the lanternfishes (family Myctophidae). Bulletin Los Angeles County Museum of Science 13:1–81.

Pearson, D. M., and T. S. Westoll. 1979. The Devonian actinopterygian *Cheirolepis* Agassiz. Transactions of the Royal Society of Edinburgh 70:337–399.

Remane, A. 1952. Die Gründlagen des naturlichen Systems, der vergleichende Anatomie und der phylogenetik. Akademische Verlagsgesellschaft Geest & Portig, K.-G., Leipzig.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes. Pp. 397–513 *in* P. H. Greenwood, R. S. Miles, and C. Patterson (eds.). Interrelationships in Fishes. Academic Press, London.

———. 1985. An essay on euteleostean classification. American Museum Novitates 2827:1–45.

———, and C. Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin American Museum of Natural History 141:357–474.

Schultze, H.-P., and E. O. Wiley. 1984. The neopterygian *Amia* as a living fossil. Pp. 153–159 *in* N. Eldredge and S. M. Stanley (eds.). Living Fossils. Springer Verlag, New York.

Springer, V. 1983. *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. Smithsonian Contributions to Zoology 390:1–40.

Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. Journal of Zoology (London) B (1) : 411–460.

Sulak, K. J. 1977. The systematics and biology of *Bathypterois* (Pisces, Chlorophthalmidae) with a revised classification of benthic myctophiform fishes. Galathea Report 14:49–108.

Taverne, L. 1977. Ostéologie, phylogénèse, et systématique des Téléostéens fossiles et actuels du super-ordre des Osteoglossomorphes. Première partie. Academie Royale de Belgique, Mémoires de la Classe des Sciences 42:1–235.

———. 1978. Ostéologie, phylogénèse, et systématique des Téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Deuxieme partie. Academic Royale de Belgique, Mémoires de la Classe des Sciences 43:1–168.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin 8:1–77.

Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei). Evolutionary Monographs 1:1–389.